STUDIES ON THE ECOLOGY OF THE AGAMID LIZARD
AMPHIBOLURUS MACULOSUS (MITCHELL)

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Summary

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Amphibolurus maculosus (Mitchell), the Lake Eyre Dragon, is restricted to arid salinas in the northern part of South Australia. The lizards live near the margins of the salinas where a suitable burrow area of fine, wind-blown sand underlies the buckled salt crust. Their essential refuge from the harsh environment is in the permanently damp sediments which occur below these dry aeolian deposits underlying the salt crust.

Preliminary laboratory experiments suggest that this lizard has a high temperature tolerance (CTM 48.9°C) and low evaporative water losses (1.1 mg/g/hr at 37.5°C).

The harvest ant, *Melophorus* sp., which occurs in the same habitat, is an important food item for the lizards, and the elevated rims of the ant nests provide shade and basking sites.

Seasonal emergence, following 3–4 months of hibernation, begins when ground temperature reaches about 19°C. At this temperature the lizards head-bask, emerging fully from the burrow when body temperature is raised to about 22°C. Under these conditions the dominant males emerge and establish territories in mid-August.

Basking postures are adopted to raise body temperature to 37.5°C (eccritic temperature determined in laboratory tests). In the field, behavioural thermoregulation maintains body temperature at about 39°C during higher air temperatures. If temperature cannot be held down within this range, the lizard retreats to the humid layer below the dry sand in the burrow zone.

Within the population, dominant, sub-dominant and subservient males can be recognised by behaviour and coloration during the breeding season (September to December). Among the females, two breeding groups, related to time of hatching, occur. Sperm retention is evident in one of these groups, in which ovulation occurs about 2 months after fertilization.

Sexual dimorphism in relation to colour pattern is not thought to be the basis of sex recognition since colour changes occur in both male and female. It seems likely that acute perception of size difference is the basis of sex recognition.

CONTENTS

1. Introduction

Amphibolurus maculosus is a highly adapted lizard, restricted in distribution to the salinas of the Lake Eyre Basin in the north of South Australia. It was first collected in 1929 by C. T. Madigan, who lodged with the South Australian Museum 20 specimens taken at the southern end of Lake Eyre North in the area now known as Madigan Gulf. These earless lizards were identified as a variety of *Tympanocryptis lineata* by H. M. Hale, then Director of the South Australian Museum (*in* Madigan 1930). In a revision of *Tympanocryptis*, a genus of "earless" dragons, Mitchell (1948) described the lizard as a new species, *T. maculosa.*

Subsequent osteological studies (Mitchell 1965) showed that the affinities of this species lie with the genus *Amphibolurus* and that it represents an extreme specialization within the genus. The enclosure of the tympanic membrane, which had led to its assignment to *Tympanocryptis*, was considered likely to be a secondarily developed characteristic. This may be an evolutionary adaptation to burrowing in dry sand, and may have arisen on more than one occasion in agamid lizards.

Lake Eyre, occupying an area of 9300 km², is the largest of several extensive salinas in the arid north of South Australia (Fig. 1), lying at the southernmost and lowest end (14 m below sea level) of the Lake Eyre Basin. This Basin lies within the 125 mm isohyet in the driest area of the Australian continent. The usually dry river systems draining towards Lake Eyre serve a catchment area of over 1,300,000 km². Some of this catchment lies within areas of comparatively heavy and regular rainfall but only under particular circumstances does sufficient water reach Lake Eyre to fill the Lake. Following exceptionally heavy summer rains in western Queensland in March 1949 and March 1950, Lake Eyre by September 1950 had filled with water for the first time in living memory. Scientific surveys, sponsored by the Royal Geographical Society of Australia (South Australian Branch) and led by C. W. Bonython, were carried out until the Lake had again dried out by November 1952 (Bonython 1955, 1956, 1960).

During this period the lizard was again observed and collected. Its ability to spend long periods foraging on the open surface of the salt crust of the Lake, withstanding both predation and desiccation, aroused considerable interest.

In 1964, Donald Campbell successfully attempted a land speed record on the surface of Lake Eyre. In order to gain access to the solid salt crust, a causeway was constructed from the shore-line across the marginal zone where the salt crust is thin. The track to the causeway permits vehicular access to the shore-line, and the causeway itself, projecting west from Prescott Point at the tip of Sulphur Peninsula (Figs. 1, 6), has subsequently served as a natural "trap" and developed a population of these lizards suitable for behavioural studies in their natural environment. A study area was set up at the causeway, where meteorological observations and records of behavioural responses of a marked population of the lizards were made during visits between February 1965 and October 1968.

This paper is based largely on field observations of the lizard on Lake Eyre, together with briefer studies of populations on other inland salinas. These field observations were supported by vivarium studies at the South Australian Museum. Preliminary experimental work is reported briefly.

2. Materials and Methods

(1) *Field Studies*

The ecological simplicity of the habitat and the lack of a predator sense in *A. maculosus* make it an attractive animal for study once problems of distance, inaccessibility and trying working conditions are accepted. The lizards are very alert and because of cryptic coloration almost impossible to detect except during their sudden, rapid movements to maintain a few metres distance from an approaching observer. During the breeding season, however, territorial challenges, fighting and mating continue uninhibited by close-range observation.

Early in the field studies some 10 km of shoreline were surveyed, but later observations were restricted to the causeway population and all meteorological records reported here were taken in that area.

In all, 16 trips were made to the study area during the period February 1965 to October 1968. Average time spent at the study area on these trips was 7 days. In addition, during September and October 1967, an extended survey was made of the major salinas extending in an arc around the northern end of the Flinders Ranges, regarded as potentially suitable habitats for the lizards.

Field data have been derived from several sources. Continuous temperature records of air and sand at various depths were obtained using an EILCO thermistorised twelve-outlet, twin channel, recording thermometer, while single readings were taken with a Thermophil electronic thermometer. Rectal temperatures were obtained with a Schultheis, quick-reading mercury thermometer, All instruments were checked and calibrated in the laboratory before each trip. Relative humidity was variously measured with cobalt thiocyanate papers,

lithium chloride cell equipment and a whirling psychrometer.

Behavioural data were obtained from direct observation and from the marking and recapture of specimens in the causeway population at Prescott Point. Quadrats were marked out along the edges of the causeway and movements of lizards in relation to these areas were recorded during the period of study. Lizards were permanently marked by toe-clipping, and colour-coded for rapid identification of marked specimens in the field.
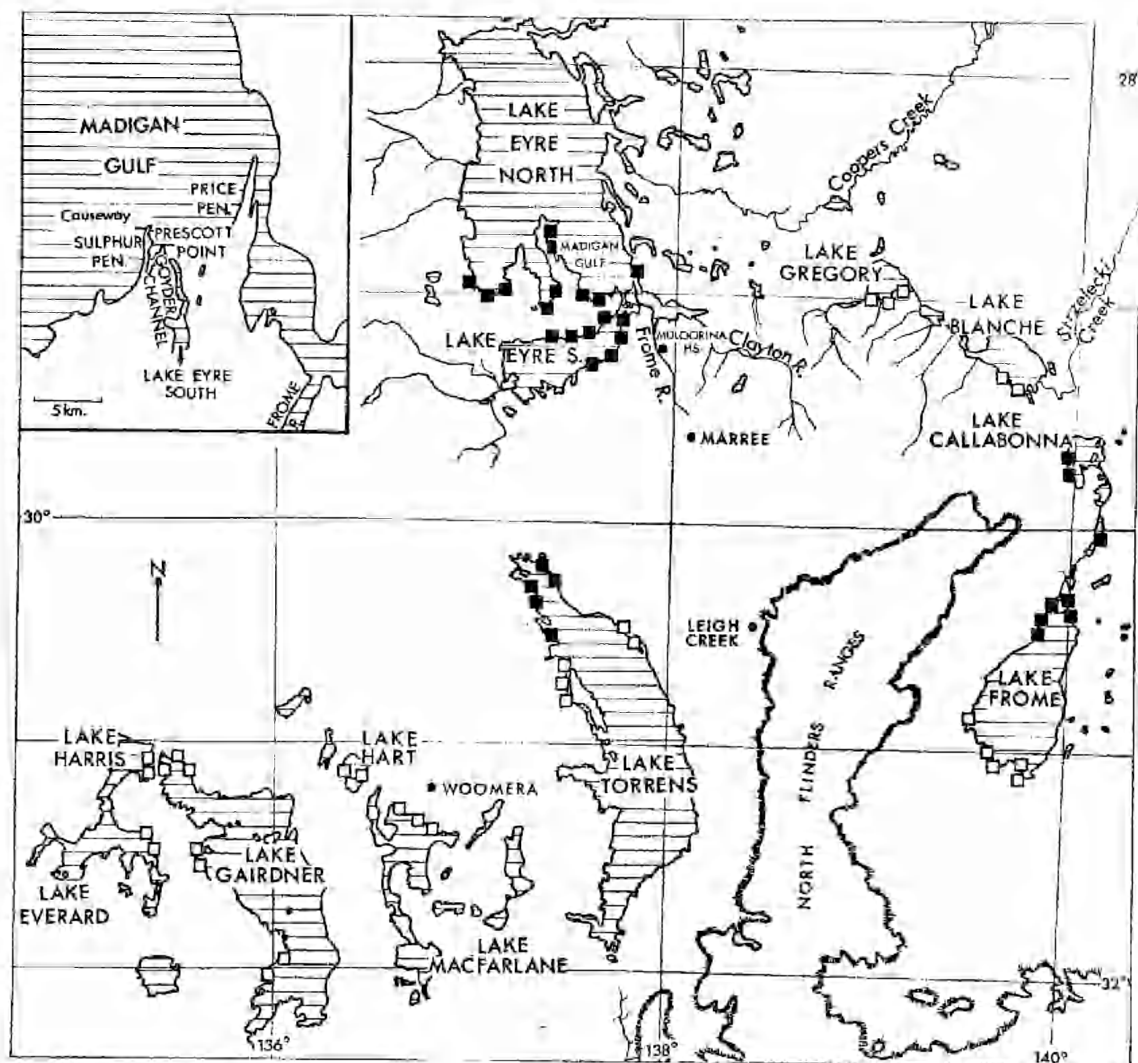
Fig. 1. Map showing the major salinas of northern South Australia and the known distribution of *Amphibolurus maculosus*. Inset map (upper left) shows portion of Madigan Gulf (the type locality), and the location of the causeway at Prescott Point which was the main study area. A *black square* indicates areas in which populations of *A. maculosus* have been observed; a *white square* indicates areas where survey of the salina margins revealed no specimens of *A. maculosus*.

(2) *Laboratory data*

Experiments on thermal criteria and temperature tolerance of *A. maculosus* were carried out in an oven preheated to 45°C. Regular temperature increments of 1°C were made at 5 minute intervals.

Rates of water loss were derived from experiments carried out in a thermostatically controlled, water-jacketed incubator under temperature conditions controlled to ±0.5°C. The test chamber was also desiccated over silica gel to ensure a relative humidity of less than 5% at all temperatures.

Experiments to determine water loss through the integument were undertaken with the vent of the animal sealed with waterproof adhesive tape and the head inserted through a thin rubber membrane across the mouth of a container partly filled with silica gel to absorb any water lost through the integument. The silica gel was overlain by a piece of thin card on which the lizard's body rested.

The test animals were acclimated for at least seven days to conditions involving the daily attainment of their maximum voluntary activity temperature (39.8°C). Animals were tested between 1000 and 1500 hours during their period of maximum activity.

For long-term behavioural studies, a terrarium was set up which successfully simulated lake shore conditions. A layer of gypseous clay, maintained in moist condition, was overlain by 15 cm of dry sand from the lake shore. Over the sand, pieces of consolidated salt crust provided a surface similar to the burrow zone area.

Both light and heating were provided by a battery of high-power incandescent lamps mounted under an adjustable hood. Time switches controlled day length, and the position of the hood controlled the maximum temperature. Strong correlation between field observations and laboratory records was found for daily and seasonal activity cycles and the onset of reproductive activities.

3. Morphology of Amphibolurus maculosus

Amphibolurus maculosus shows several features of morphology, physiology and behaviour which reflect its adaptation to arid salinas. Its dorsal surface is white to very pale grey with a row of very dense black blotches on either side of the vertebral line. Dorsally and laterally there are smaller black and rusty-brown pigmented areas. This colour pattern gives excellent cryptic colouration on the salt surface, the dark areas blending with the shadows of small holes and pinnacles on the rough salt (Figs. 9, 10, 15). The ventral surface is white with a dark streak extending longitudinally along the centre of the throat to the gular fold. Colour variations related to the environment, and the striking colour patterns developed during the breeding season will be discussed later in this paper.

The adult male attains a total length of about 11.5 cm (snout-vent length 7 cm), the adult female being smaller at about 10.0 cm (snout-vent length 6 cm).

The eye is small and deeply sunken and is protected from salt glare by prominent serrated eyelids with dark pigmented linings (Fig. 4). The nostrils, while showing a circular external opening, open into the nasal cavity by only a narrow slit, directed forward and downward. This structure prevents the nasal passages from becoming blocked when the lizard burrows through loose sand. Special nasal structure has been described by Stebbins (1943) in the American genus *Uma*, which is a sand-burrowing form. He has shown (Stebbins 1948) that other American iguanid genera including *Uta*, *Holbrookia* and *Phrynosoma*, all of which habitually burrow in loose sand, have similarly adapted nasal structure.

4. Habitat and Distribution

The type locality of *A. maculosus* is Madigan Gulf, Lake Eyre North, out from the mouth of the Frome River. The species is widely distributed around the southern shoreline of Lake Eyre North and around the northern and south-eastern shorelines of Lake Eyre South. Throughout the study every opportunity was taken to search other lakes for additional populations and practically all of the major salinas in the State were at least cursorily examined for signs of habitation by these lizards. Two additional populations were found: a population in the saline areas at the southern end of Lake Callabonna and extending southwards through the salt channels into the northern tip of Lake Frome, and another population along the north-western shoreline of Lake Torrens. Fig. 1 shows the area searched, the localities from which specimens have been taken, and the range over which this species is known to occur.

The geomorphology and the history of landforms in the Lake Eyre Basin have been discussed by Wopfner & Twidale (1967). Evi-

dence from fossil deposits suggest that extensive areas of brackish water or saline swamps existed within the basin from mid-Tertiary to the end of the Pleistocene. The origin of the salt in Lake Eyre has been subject to debate but it seems likely that both cyclic salt and connate salt, accumulated from waters brought into the basin from the extensive drainage system, have contributed (Bonython 1956; Wopfner & Twidale 1967; Twidale 1968). The present isolated populations of *A. maculosus*, which although spatially widely separated are virtually morphologically indistinguishable from one another, may be relict from a more widespread species evolved in association with the shore-lines of the large brackish lakes and swamps that were a feature of the Lake Eyre Basin during Pleistocene and early Recent periods.

THE HABITAT OF THE LAKE EYRE POPULATION

The habitat within the study area can be divided into three distinct zones, the "beach", the "burrow zone" and the "wet salt zone" (Fig. 5). This zonation can be readily identified throughout the distribution of the Lake Eyre population examined, but is much less distinct in the area of the other two populations.

1. *The beach:* In the area along the southern shore-line of Lake Eyre North which was most intensively studied, the beach is backed by near-white sandhills varying from low consolidated hummocks stabilised by low shrubby vegetation (*Nitraria, Scaevola*) to high drifting dunes encroaching upon the lake. In many areas low cliffs varying in height from about a metre to approximately 12 m above the lake bed expose Recent to Cretaceous sediments to face the lake. Continuous wind erosion transports large quantities of gypsiferous clay and grit and other aeolian fines out over the beach and on to the surface of the lake. The beach is usually a narrow strip of consolidated sand frequently intermixed with areas of very coarse sand and pebbles. In areas where it is not overlain by recent drift it remains damp during the cooler months. Typical pebble beaches occur in some areas and the height and form of some of these beaches suggest sustained periods of strong wave action in the very recent past.

2. *The burrow zone:* This term has been adopted to cover the zone in which most of the activity of the lizards takes place. It consists of an area of distorted, dry, crusty sur-face, varying from a few metres wide (in areas where flooding approaches close inshore or where little gypsiferous drift is brought out by the prevailing wind) to 400–500 m wide in seldom-flooded embayments where wind-drifted deposits have accumulated on the surface (Fig. 5). This 5–15 cm thick layer of fine gypsiferous clay and sand rapidly dries out and in doing so expands and distorts the salty crust which forms over the top of it. In section, this provides a burrowing substrate consisting of an irregular, salt-impregnated, crust up to 2 cm thick, lying above approximately 10 cm of fine, dry, windblown sediments underlain by sand which is kept continually damp from the water-table 40–70 cm below.

The lizards break through the salty crust at a weak point and then literally "swim" through the fine mobile sediments below until they encounter the high humidity associated with the damp consolidated sand at lower levels. They remain there until their re-emergence is triggered by rising temperatures or some internal stimulus. They follow the thermal gradient back to the surface, frequently emerging at a different point to that of entry.

3. *The "wet" salt zone:* The solid salt crust of the lake varies from about 2 cm in thickness in inshore areas to about 40 cm in thickness towards the centre of Madigan Gulf. This crust, overlying wet gypseous clay, becomes distorted and buckled as the salt recrystallises on drying out (Figs. 7, 8). Although most of the activity of this lizard takes place within 250 m of the shore, both the lizards and the nests of the ant *Melophorus* sp. (their principal item of food) have been observed more than 1400 m from the shore line. During the territorial season, many young subordinate males are forced to live outside the burrow zone and are frequently found well offshore. While little weight can be placed on the salt surface without bringing water to the surface, the actual surface "skin" is dry most of the time except in certain efflorescent areas close to shore which are continually damp. Relative humidity readings using cobalt thiocyanate papers set 1 cm off the salt under a shield, gave readings as high as 55% over these efflorescent areas, but in other areas the reading was below 15% and equalled the reading at 100 cm above the surface.

THE LAKE CALLABONNA POPULATION

Essentially the same conditions prevail as at Lake Eyre, with the lizards living around the

southern margins of the lake on isolated patches of aeolian drift in association with dry saline crust. A suitable habitat is not present in northern parts of the lake, where fresh water from the Strzelecki Creek has leached the bulk of the sodium and calcium salts from the surface deposits and the water table is deeper because of extensive Recent lacustrine deposits on the surface.

THE LAKE TORRENS POPULATION

The surface of Lake Torrens is wet and muddy and the lake frequently contains water. As a consequence the population has adjusted its behaviour to living among low vegetation along the immediate shoreline and upon low-relief islands covered with chenopodiaceous shrubs.

PHYSICAL FEATURES OF THE BURROW ZONE

Field and laboratory observations suggest that there are three essential habitat characteristics which influence the distribution of this lizard.

1. *A surface crust:* Specimens placed in a laboratory cage containing either loose sand or consolidated sand lacking a surface crust were unable to burrow. They were only able to scoop out a shallow depression. Several field observations related to this were made during the 1952 flooding of the lake when most of the lizards were forced onto the damp beach. Some did succeed in finding crusted areas back among the vegetation but several lizards were found in shallow depressions against driftwood along the beach. Presumably the surface crust is essential in providing initial purchase against which these lizards start their "swimming" procedure in burrowing through the sand. The consolidated surface crust need not necessarily be saline and in fact, gypsiferous sediments bound together by filamentous blue-green algae may well have provided a suitable habitat surface over wide areas in the past and may prove to be a contributing factor at present.

2. *A layer of fine dry sand (and/or clay) about 10 cm thick under the crust:* In order to provide adequate insulation from the extreme heat of the summer, the fine sand or sand-gypsiferous clay mixture must be dry and about 10 cm thick. It is probably important that the sediments contain gypsum to promote expansion and rapid drying after wetting.

3. *A constant source of humidity for the retreat:* Because of the water balance problems inherent in living upon a salt surface subject to extreme temperature, it is essential that the environment provide a refuge in which both evaporative and respiratory water losses be minimised during the periods of retirement underground. The sediments at about 10 cm below the surface crust must be permanently damp.

PRESENT KNOWN DISTRIBUTION

At most of the localities examined along the shore of Lake Eyre North and Lake Eyre South, lizards (or signs of their presence) were observed whenever a combination of the three factors described above were found. This applied equally well to Lake Callabonna except that suitable habitat there is much more limited. Most of the northern part of Lake Callabonna and Lakes Blanche and Gregory have a very friable surface deposit of fine gypsiferous clay which is not bound by a surface crust. This is not a suitable habitat. Lake Torrens lies on the "weather" side of the Flinders Ranges and is therefore subject to more frequent flooding than the other lakes around the northern end of these ranges. The lake surface is therefore permanently wet and does not provide a suitable habitat, but at the northern end and particularly along the western side, suitable conditions occur along the actual shoreline and upon low insular areas where the pale gypsiferous clay supports sparse halophytic vegetation. Many of these areas dry out during the warmer months, and form a suitable habitat with a distinct surface crust underlain by varying depths of dry pale yellow to red gypsiferous clayey silt. This habitat is exploited by the Lake Torrens population. Specimens have been collected up to 275 metres back into the vegetated zone away from the margin of the lake.

Other lakes examined were Lake Harris, Lake Gairdner, Lake Everard and Lake Hart (Fig. 1). Although knowledge of the shoreline conditions gained during this survey was very fragmentary, the general information gathered is considered adequate to suggest that if any additional populations are found on any of these lakes, they will not be found living upon the surface of the lakes as at Lakes Eyre and Callabonna, but along the margins as at Lake Torrens. The surface conditions of these Lakes are similar to Lake Torrens, the surface being too wet to support the ants

(*Melophorus* sp.) which provide the principal item of diet for these lizards; these ants, or other species of similar burrowing habit, are restricted to the shore-line areas. In many of the lakes, the ecological situation occupied by the ants at Lake Eyre is taken over by a species of Fighting Spider (*Geolycosa* sp.). Cicindeline beetles are also frequent and active predators over these damp lakes and in part replace the ants as surface scavengers. They dig vertical burrows into the damp muddy surface and have only been seen at the Lake Eyre study area when layers of fresh silt from floodings were overlying the salt.

5. Microclimate of the Habitat

A. maculosus has a strict preference for the margins of the salinas and does not invade the white sandhills despite its competitive dominance, in cage experiments, over the only agamid species which occurs there (*Amphibolurus pictus* Peters). It was noted also that *A. pictus* makes burrows over a metre long and up to 20 cm deep in mid-summer, despite the fact that its thermal tolerances are only slightly inferior to those of *A. maculosus* (see Table 2). This suggested that the lake surface environment may have some thermal advantage over the adjacent sandhills. Climatic conditions prevailing within the habitat were studied in an effort to determine the reason for the strict habitat preference and also to provide a foundation for an analysis of the activity and behavioural patterns observed.

(1) *Temperature*

Using the thermistorised recording thermometer, an attempt was made to compare the temperature profiles of the sections of the burrow zone preferred as a refuge by the lizards with parallel situations in the adjacent sandhills. Comparison between summer (February) and winter (July) temperature patterns for both the burrow zone area and the nearby white sand-dune area is given in Fig. 2. Summer soil temperature profiles for burrow zone and sand-dunes are shown in Fig. 3. The data obtained proved difficult to evaluate, probably because of the difficulty of obtaining strictly comparable test sites. The ground humidity varies from place to place with the local soil structure conditions and the thickness of the surface drift, and the extent to which the ground water has penetrated towards the surface also varies. It is

not possible to assess these factors without breaking the surface crust and thereby disturbing the stratification of the protective layers under which the lizards normally rest. Therefore, while the lizards were found consistently to prefer to rest on or just in the damp sand underlying the mobile dry sand, it was seldom possible to determine when the tip of the thermistor probe was lying in this same position. Also the protective value of the surface soil was greatly reduced by local rain which increased its conductivity. All of these factors reduce the comparative value of the data.

The data, however, do allow two conclusions to be drawn with reasonable confidence. Firstly, during the cooler weather when both the burrow zone deposits and the adjacent sandhills are damp to the surface, the thermal characteristics are essentially the same. Secondly, in midsummer the temperature at average refuge depth (10 cm) in the burrow zone, probably due to the thermal capacity of the water table 40–70 cm below, is lower and subject to less fluctation ($30 \pm 1.5°C$) than the temperature in an equivalent situation in the adjacent sandhills ($34 \pm 4°C$) (Figs. 2, 3).

(2) *Humidity*

Surface temperatures were recorded using a contact thermistor and a Thermophil electronic thermometer. Because of the saturation of the lake floor right to the surface and the periodic appearance of free water on the surface of the more thickly salt encrusted area, it was anticipated that evaporative cooling would contribute to lowering surface temperature of the lake and raising humidity, particularly at the "living level" of the lizards (1 cm), both being features which would improve its suitability as a habitat during the warmer months. However, careful testing with the thermistor probe revealed the actual surface of the "wet" salt to be dry and at the same temperature as the crust in the burrow zone and the sand in the sandhills. Similarly, tests with cobalt thiocyanate humidity papers at 1 cm and 100 cm above the lake surface and 100 cm above the adjacent sandhill surface usually gave the same reading. Over the temperature range 30 to 40°C, during which lizards could be expected to be active over the "wet" salt surface, the readings were usually below the minimum sensitivity of the paper, indicating relative humidities below 15%.

Humidity readings, derived from each of the sources described above, varied from less than 5% to 55% relative humidity. The higher readings invariably followed light rain or thundery conditions and were the same for sandhills and lake surface sites. As air temperature increases each day, over the solid salt crust, the "wet" salt begins to "sweat" and brine appears at the tips of small, self-sealing, salt pinnacles. Due to the high temperatures and high evaporative rate it is likely that any humidifying effect of this brine is restricted to a micro-layer, of perhaps only a few mm, just above the evaporative surface. However, it was not possible to detect higher humidity over the "wet" salt surface and this is possibly due to inadequate instrumentation.

(3) *Salinity*

The salinity of the wind-blown silts deposited in the burrow zone varies with depth. Salts dissolved out from the superficial layers were 7–11% of the silt; 3–5 cm down, 4–8% and 5–10 cm down, 3–4%. Below this level the salinity steadily increases again up to saturation at the water table 40–70 cm below the surface. The decrease in salinity nearer the surface is probably due to the recent origin of the surface deposit and to condensation along the line of demarcation between the permanently dampened sands and the overlying dry sediments leaching the salt out over a period of time. The lizards normally rest in this zone of lower salinity but whether this is of any advantage is unknown. The sand along the foreshore also contains 2–4% salt and the observed salinity stratification may be due to an increase in surface salinity by wind drift from the sandhills rather than to desalination of the intermediate layers.

Several small areas of white efflorescent salts were found just outside the burrow zone and these areas are continually losing water to the atmosphere. Although no lizards were ever observed using one of these areas on a hot day, the large number of fecal pellets present on and around them suggest that their thermal advantages may be utilised by the lizards. The surface temperature of such an area of about 3 m² near the main study site was compared with that of the surrounding salt and found to be up to 9.5°C lower.

It appears that the lake surface confers no advantages upon an inhabitant, either in terms of surface temperature or humidity, over the condition prevailing in the surrounding sandhills. Despite the abundance of free saline water throughout the habitat it may still be inadequate to prevent the high evaporative rate [about 220 cm per annum (Bonython, 1955)] from creating sufficient dry hygroscopic salt throughout the habitat to place greater strain on the water balance of this species than other desert-adapted lizards.

The permanently damp layer under the protective crust in the burrow zone provides a high humidity retreat into which the lizards can retire overnight or, if under social or environmental stress, for much longer periods without endangering their water balance. This is regarded as the key factor in restricting the species to the marginal areas of the salinas.

6. Food and Predation

The main food source for *A. maculosus* is the harvest-ant, *Melophorus* sp. In addition to providing food, the nest-mounds of these ants are important "features" in the generally featureless habitat, providing lookout points, basking sites and the only source of shade.

Colonies of *Melophorus* generally occur on the "wet-salt" surface usually within 750 m from the beach zone; preference is shown for areas where the salt-crust is no more than 2 cm thick and underlain by relatively clean sand down to the water-table 40–70 cm below. The colonies are regularly spaced over the lake surface, each being about 10 m equidistant from the next (Fig. 8). Investigation of a nest revealed a series of upper galleries just beneath the salt crust and a single vertical hole going down about 40 cm to a second set

Fig.   2. Comparison between summer and winter thermal characteristics of the burrow zone and adjacent white sand dunes. Figures from continuous recorder traces of temperature were plotted at 30 minute intervals.
————— temperature at –10 cm
--------- temperature at –1 cm
. . . . . . air temperature at 40 cm above ground
(A) Burrow zone temperatures over 34 hour periods in February, 1965 and July, 1966. Temperature range at –10 cm for the February period was 3.5°C, about a mean of 33.6°C.
(B) Sand dune temperatures over 34 hour periods in March, 1965 and July, 1966. Temperature range at –10 cm for the March period was 11.5°C, about a mean of 34.6°C.
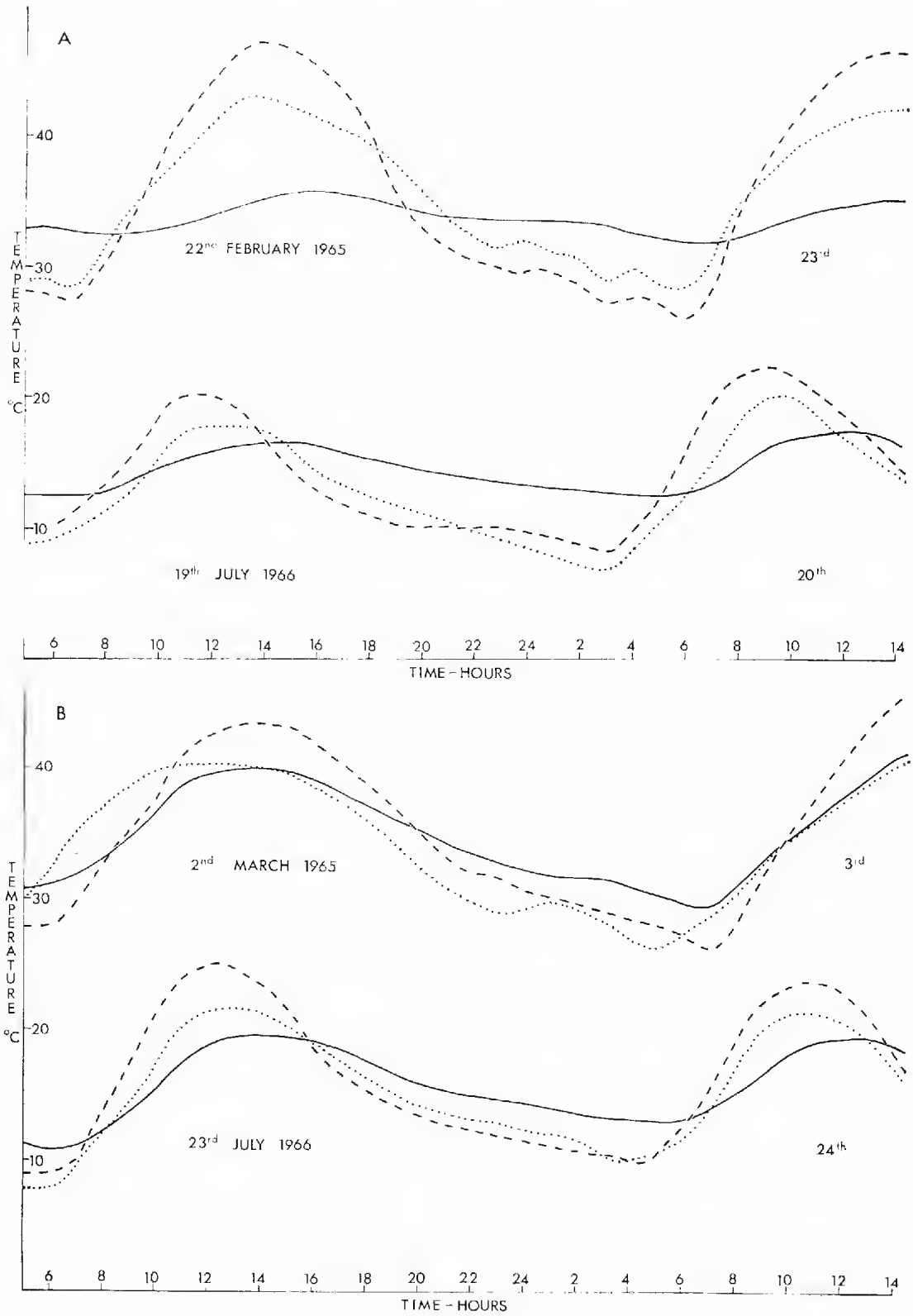
FIG. 2

of galleries at or along a consolidated layer of clay just above the water-table. The construction of these galleries produces, on the surface, a distinctive crateriform mound up to 20 cm in height. The sand below the salt crust is usually covered by a fine layer of clay which probably accounts for the reddish-brown debris, brought from below, being in marked contrast to the white salt crust.

At any time, only a small proportion of the total number of nests contain active colonies. The ants show limited activity during the day, appearing at the surface only to deposit sand grains from the workings below ground.

In view of the limited above-surface activity of the ants, it has been suggested (Madigan 1930) that *Melophorus* harvests micro-organisms either in the salt crust (blue-green algal cells) or in the damp sand above the water table (*Dunaliella* spp.). The nests usually, however, contain insect remains and the ants have been observed gathering bodies of insects trapped on the salt. Probably most foraging activity by the ants occurs at night.

A. maculosus, also, is an opportunistic feeder and when other insect life is available on the lake surface, the lizards feed on a wide range of different insect species. On most nights numbers of insects are stranded on the salt surface. Their presence may be explained in several ways. With an offshore wind many insects may be blown out over the lake; others may be attracted by the rise in humidity over the lake surface at night; aquatic insects (particularly on moonlit nights) may mistake the white lake surface for water. Overall the lake surface produces a vast "white sheet" effect — a commonly used form of insect trap—and many insects are trapped on the hygroscopic salt surface and killed when temperature increases next morning. During the spring months, September–November, vast quantities of insect life may occasionally be stranded on the lake surface. The bodies of insects which have been neither captured by *A. maculosus* nor later scavenged by *Melo-*

phorus become incorporated within the surface salt layers.

It is of interest that the characteristic insect fauna developed in the vegetation of the shore-line and sand-hills is rarely stranded on the salt surface of the lake, while the majority of species stranded on the salt are seldom seen about the shore.

The period of greatest feeding activity of *A. maculosus* (February to April) frequently coincides with drought conditions in the surrounding country, and consequent limited supply of windborne insect life.

In view of the limited number of ants active on the surface, the lizards must forage out over the lake surface for long periods at high temperatures. The lizards dig into the sides of the ant nests to retrieve ants from inside, and the more frequently visited ant-nests closer inshore become very battered in appearance. Shallow depressions scraped out at the base of the nests provide small areas of shade into which the lizards may retreat.

The Lake Eyre population of *A. maculosus* displays no response to overhead predators, relying for safety on their cryptic coloration. The only possible protective cover on the lake surface is provided by buckles and cracks in the surface of the salt crust (Figs. 7, 13). Although these would seem to provide ideal retreats they are rarely used by the lizards. The crystalline salt in the crust provides a "glasshouse" effect and the temperature below the crust may be several degrees higher than the surface of the salt. When pursued over the surface until exhausted, the lizards are more likely to come to rest in the shade of the pursuer than to retreat below the salt crust. There is little evidence of other potential predators moving out across the salt surface.

Hawks constitute one of the main predators of *A. pictus* from the sandhills adjoining the lake. On several occasions dead specimens of *A. pictus* have been observed well off-shore on the lake surface. Presumably these have been dropped by hawks. The fact that these

Fig. 3. Tautochrones (soil-air temperature profiles at different times during the day) recorded on 6th March, 1965 for (A) burrow zone area and (B) sand dune area. Differing thermal characteristics of the two localities result in the more rapid and greater heating in the sand dune area. At −10 cm (average burrow depth of *A. maculosus*) in the burrow zone there is a temperature range from 30.9 to 35.6°C over the time period recorded. At the same depth in the sand dune area there is a temperature range from 31.4 to 41.4°C over a similar time interval. In (B), due to the limited range of the thermometer used (calibrated up to 120 F (49°C)), no figures are available for the 2 cm and 4 cm depths at the 1120 and 1515 readings. Field notes recorded that, at these times and depths, the temperature was "120°F+ and rising rapidly".
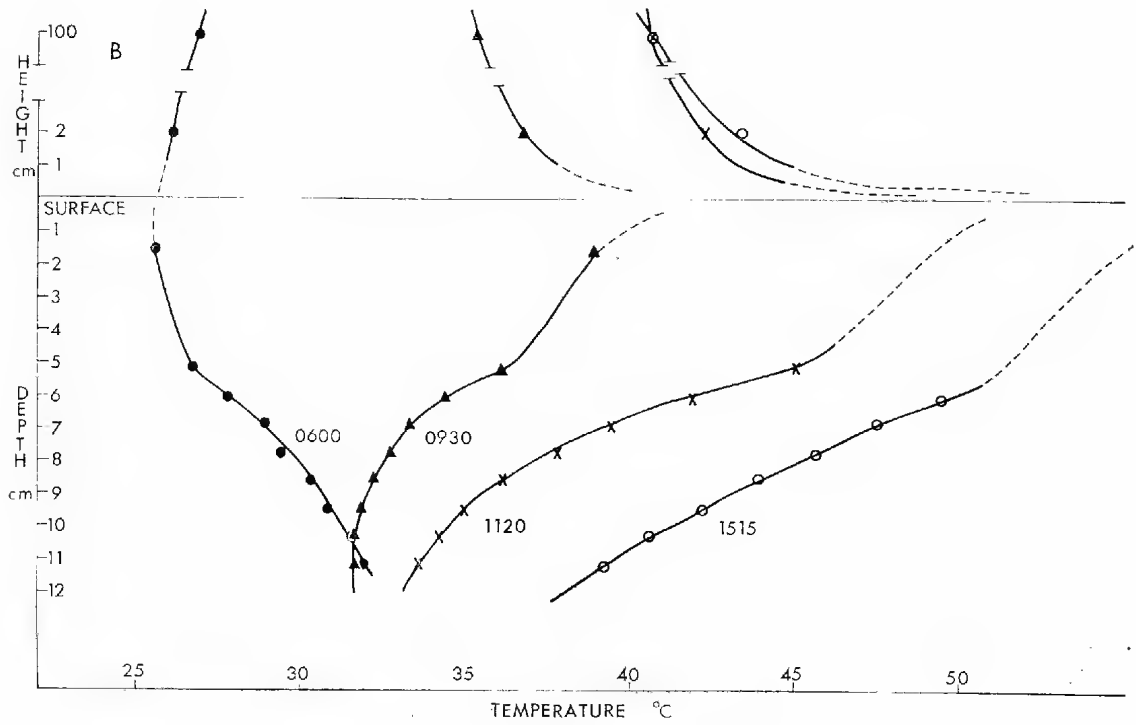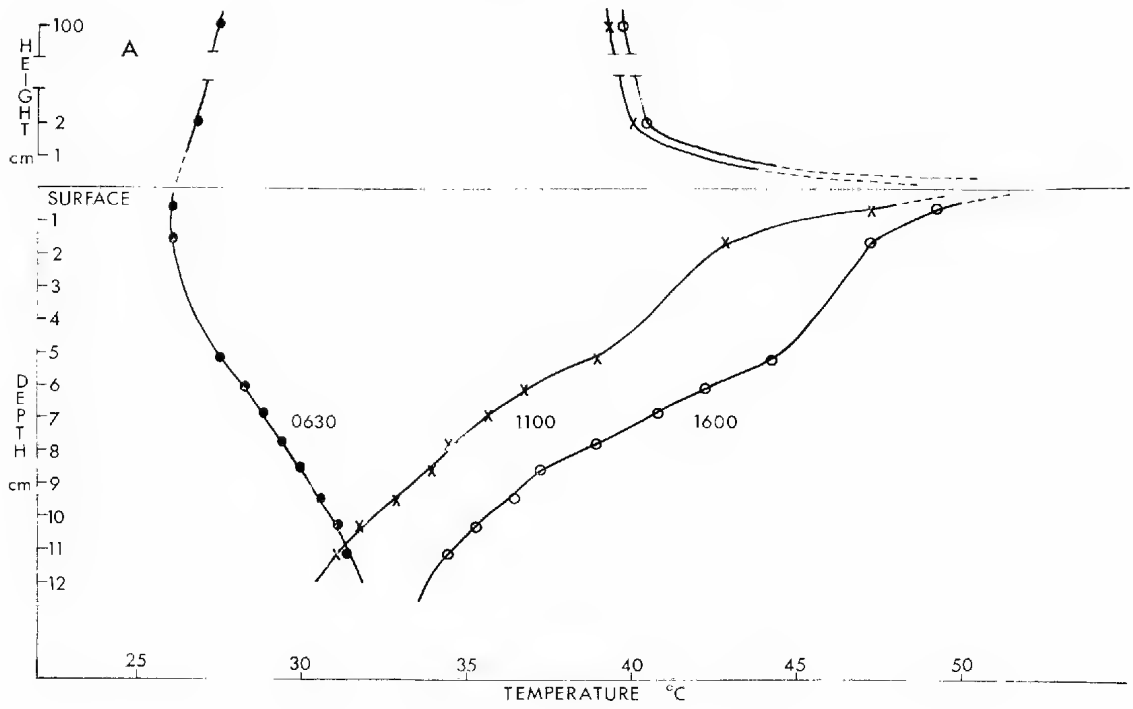
FIG. 3

captures have not been retrieved would sug-
gest that the glare from the lake surface may
confuse aerial predators.

7. Flooding of the Habitat

The periodic flooding, either of the whole
of Lake Eyre or, following more localised
rains, of restricted areas, must affect both
Melophorus and *A. maculosus.*

Melophorus colonies withstand flooding for
considerable periods by becoming sealed off
below the water. As water disappears from
the lake surface, the colonies soon "break
out" and rework the galleries and nest. The
shape of the above-surface mound would give
protection to the opening of the nest during
light flooding.

When the normal burrow zone is flooded,
A. maculosus retreats to the shore line and
lives, precariously, in the sand there. The
lizards are frustrated in attempts to retire
underground since there is no consolidated
crust to provide leverage for burrowing, and
they have no refuge from predators such as
the Ground Goanna (*Varanus gouldii* Gray)
against which they have adequate protection
in their normal habitat. Among the lizards
forced ashore by flooding, colour changes
occur in which the background colour of the
lizard becomes a deeper grey and the areas of
black and rusty-brown pigmentation become
more numerous and intense, giving a
speckled appearance more similar to the pebbly
beach sands. At times of flooding, large num-
bers of Silver Gulls (*Larus novae-hollandiae*
Stephens) are attracted to the area and these
probably constitute the greatest predation
hazard for *A. maculosus.*

An interesting response to flooded conditions
has been observed in *A. maculosus.* During
winter at low ground temperatures (down to
16°C) the lizard is in torpor. In vivarium
experiments at low ground temperatures (14–
16°C), flooding of the substrate aroused lizards
which had been below the surface in torpor
for 3–4 weeks. Emergence to the surface
involved a greater degree of muscular co-
ordination than is usually shown at these
temperatures and may be triggered by lack of
oxygen. Inflation of the body when it emerges
from underground ensures that the lizard floats
on the surface of the water. It would appear
possible that such a reaction would assist
survival of the animal in face of encroaching
floodwaters.

Localised areas of water in the lake show
marked response to changes of direction and
velocity of wind. A flooded inshore area may,
within a few hours, appear as an exposed
salt surface and vice versa. This must impose
additional problems in the re-establishment of
both *Melophorus* and *A. maculosus* in their
preferred habitat.

8. Activity patterns and Thermoregulation

Like other ectothermic animals, the activity
of *Amphibolurus maculosus* depends on
temperature. The lizards show definite be-
havioural responses at certain temperatures
and these responses serve to keep the body
temperature within a preferred activity range.
Throughout the season of lizard activity, varia-
tions occur in the means and ranges of these
temperatures. These variations, imposed by the
age and sex of the particular lizard and its
position in the social structure of the popula-
tion, are considered later. The basic range of
temperatures associated with various activities,
summarised in Table 1, is dicussed here.

During the winter months (May to August),
A. maculosus remains in torpor below ground.
Emergence threshold air temperature is 19°C,
at which temperature there is early season
emergence (August–September), under stress
of hunger and drive for the establishment of
territory, in males. At this temperature only
the head of the lizard is thrust through the
salt crust. It is darkly pigmented in the pineal
region and the eyelids are extended, indicat-
ing accumulation of blood in the cephalic
sinuses. The morphology of venous shunts in
the cephalic region, and their role in head-
body temperature regulation, have been
described for *Phrynosoma cornutum* by Heath
(1964, 1966). Although the anatomy of the
head of *A. maculosus* has not been examined,
there is similarity in head-basking behaviour
between this lizard and *Phrynosoma*, which
is known to use this aid to rapid stimulation
of the central nervous system and elevation
of body temperature. It seems likely that *A.
maculosus* uses a similar mechanism. The
head-basking position is only maintained until
the body temperature is raised to 22°C, at
which temperature the body is fully exposed
at the mouth of the burrow. It is at this tem-
perature that most lizards first emerge for
the season in September–October. During
early basking stages the body of the lizard
is orientated with the back exposed to the
sun (or source of heat in the vivarium), and
the body is inflated laterally and closely

pressed to the substrate, with the hind legs spread out flat behind the body in a "swimming" position.

Under laboratory conditions, with air temperature at 23°C, the adult lizards emerged, with eyes still closed, as soon as the lights came on. Within 10 minutes all were fully emerged and awake in the flattened basking position. Within 30 minutes rectal temperatures had risen to 30°C at an air temperature of 23.9°C.

During summer, mean burrow temperature (at about 10 cm depth) is 32°C. Under these conditions daily emergence occurs with first light, and temperature is no longer the controlling factor.

The basking position is maintained until body temperature reaches 26–27°C, when the lizards first start to move away from the burrow and are sufficiently co-ordinated to feed.

At a body temperature of 32°C, the lizards are capable of full range of movement and activity and, in hot weather, they move out onto the salt crust at this temperature. The eccritic or preferred body temperature, was determined in the laboratory by use of a sawtooth thermocline. Under laboratory condi-

tions the top temperature of the basking range is 37.5°C. At this temperature there is re-orientation of the lizard from the positive to negative with respect to heat source.

In the vivarium, the lizards can retreat under-ground at any time, whereas in the lake habitat, they must return from the wet salt surface to the burrow zone to retire underground. In the vivarium they retreat underground at a body temperature of 37–37.5°C, while in the field they remain active on the salt surface away from the burrow zone with body temperature held at about 39°C.

Except under very hot conditions, the lizards have a normal activity cycle of about 8 hours per day. This long period of scavenging is correlated with food supply and is necessary to ensure that they obtain sufficient food. In summer, during much of this time air and surface temperatures would be over 45°C. At these temperatures the body of the lizard is held high off the salt surface, the only points of contact with the hot surface being the feet and end of the tail. If stationary for any length of time, the toes of the hind feet are raised from the surface so that there is contact only with the limited area of the heel.

During thermoregulatory maintenance of body temperature at about 39°C, use is made of the diversity of substrate conditions provided by the buckled salt crust, of the small areas of shade cast by the ant nests and of the few small pieces of driftwood embedded in the salt surface which are used as elevated perches.

Since, during the hotter summer months, there is an established behavioural pattern of daily movement out from the burrow zone onto the "wet" salt crust as the temperature rises, it seems likely that the lizards achieve some thermoregulatory advantage in this area.

While measurements revealed no consistent decrease of temperature or humidity over the "wet" salt, this may simply reflect the technical difficulty of detecting small changes on the actual surface of the crust.

Slight pressure on the "wet" salt crust releases moisture to the surface, accompanied by a rapid, transitory fall in temperature due to evaporative cooling (particularly when a wind is blowing). The lizards, by scratching at the surface of the crust, may achieve this same cooling effect for parts of the body in contact with the surface. It is noticeable that

TABLE 1

Activity of A. maculosus *in relation to body temperature*

Temperature	Activity	Category
50°C		
	–49.5°C—lethal temperature	uncontrolled heating
	–48.9°C—CTM	
45°C		
	–42–43°C—panting	thermoregulatory temperature control
40°C	–39C—controlled temperature (field)	
	–37.5°C—eccritic temperature (lab.)	
35°C		
	–32°C—full activity	
30°C		
	–27–28°C—move from burrow	basking range
25°C		
	–22°C—full emergence	
20°C		
	–19°C—early emergence; head basking	

during the hot months, which coincide with the defence of territory by the dominant males, the young males forced to spend considerable time out over the salt surface develop accumulations of salt on the digits of all limbs (Fig. 11). There may also be salt encrustation along the ventral surfaces of these lizards. This salt accumulation may be caused by the lizards scratching at the surface of the salt crust in attempts to benefit from any slight evaporative cooling effects.

When no longer able to control body temperature by adjusting position and stance, the lizard must retreat to the burrow zone and retire underground. In order to reach the cooler, wet sand layer near the water table, the lizard must first penetrate the loose sand below the salt crust. The upper layer of this loose sand may reach a temperature of 60°C. *A. maculosus* must have a short-term tolerance to this extreme temperature in order to benefit from the humid layer below.

If forced to remain active at higher temperatures, *A. maculosus* begins to "pant" at a body temperature of 42–42.5°C. In this action the mouth is opened wide (Fig. 10), and there is a steady rate of deep breathing at 60 breaths/minute. Unlike some other lizards (e.g. *Varanus* spp., *A. pictus*, *A. inermis*) there are no associated movements of the gular pouch during panting in *A. maculosus*.

Tolerance of temperatures above 42°C, at which thermoregulation begins to break down, are discussed below.

Preferred body temperatures and thermoregulatory behaviour of several other species of *Amphibolurus* have been described by Bartholomew & Tucker (1963), Bradshaw & Main (1968), Brattstrom (1971), Heatwole (1970), Lee & Badham (1963), Licht, Dawson, Shoemaker & Main (1966), and Pianka (1971 a, b).

9. Survival in the Preferred Habitat

The habitat preference of *Amphibolurus maculosus* is unique among vertebrate animals and many factors would appear to count against survival in such a harsh, extreme environment. There are obvious problems in maintaining water balance, arising from the hygroscopic salt surface on which the lizard

spends much of its time, compounded by lack of access to free water from which to supplement its supply, and the need to handle a higher than average sodium intake. (The ants, *Melophorus* sp., have a high salt content (Braysher 1972[1]) and many of the insects trapped on the lake surface have salty encrustation on their body and legs). The survival of an insectivorous animal in a vegetation free habitat, periodic flooding of the lake, high summer temperatures, and lack of cover from the sun, are all matters which require special physiological or behavioural adjustment.

However the lizard has the ability to exploit this habitat successfully. The low rate of reproduction (one to four eggs per female per annum) suggests that its biology is more than adequate to meet the environmental stresses. As with all desert-adapted animals, behavioural avoidance of environmental extremes (Schmidt-Nielsen 1964) has been shown to be a key factor in survival in this harsh environment, but the study also indicated that the environmental stresses encountered require considerable physiological adjustment to ensure survival. The wide scope of this study has only permitted superficial examination of these adaptive mechanisms, and more detailed studies have been undertaken by other workers.

Tolerance to temperature and water stress

Survival of *Amphibolurus maculosus* in the Lake Eyre habitat involves ability to withstand high temperatures and to cope with the lack of free water.

Preliminary experiments were carried out to determine some of the thermal criteria and rates of evaporative water loss. Although the results are based on very few readings, the data are presented here since they are the only records available for this species. Comparison is made with published data for two other species of *Amphibolurus*: *A. pictus* Peters and *A. inermis* (De Vis). Both of these species are widely distributed in desert areas and occur in the sand dune country adjacent to Lake Eyre. *A. inermis* is generally found in red sand and *A. pictus* shows preference for white sand. Comparisons between *A. maculosus*, *A. pictus* and *A. inermis* are summarised in Table 2.

[1] BRAYSHER, M. I. (1972).—Water and electrolyte balance in the agamid lizard *Amphibolurus maculosus* (Mitchell), and the structure and function of the nasal salt gland of the sleepy lizard, *Trachydosaurus rugosus* (Gray). Unpublished Ph.D. Thesis, University of Adelaide.

TABLE 2

Thermal criteria and rates of evaporative water loss for A. maculosus, A. pictus *and* A. inermis

	A. maculosus	A. pictus		A. inermis					
	Mitchell, present study	Mitchell, present study	Warburg (1965b)	Mitchell, present study	Warburg (1965b)	Licht, Dawson & Shoemaker (1966)	Bradshaw & Main (1968)	Heatwole (1970)	Bradshaw (1970)
Eccritic temperature	37.0°C								
CTM	48.9°C	46.5°C	45°C	48.5°C	46.5°C			48.5°C	
Lethal temperature	49.5°C							49.3°C	
Survival	390 min. at 45°C		240 min. at 42°C		480 min. at 44°C	103 min. at 46°C	62±6.48 min. at 46°C		
EWL	1.10 mg/g/hr at 37.5°C		1.58 mg/g/hr at 37.5°C		0.85 mg/g/hr at 37.5°C				1.05 ± 0.0913 mg/g/hr at 35°C

The critical thermal maximum (CTM), defined by Cowles & Bogert (1944) as that temperature at which a reptile loses muscular co-ordination, has been determined for a number of Australian lizards (Warburg 1965 b; Heatwole 1970).

Comparisons between these data are difficult to make because of differences in experimental procedures. Also, the usefulness of this thermal criterion has been criticised because some lizards, after losing muscular co-ordination and passing into a coma, are capable of recovery if held at that temperature or if the temperature is lowered. Other lizards do not recover after these muscular spasms and die quickly, or within a few hours.

The CTM for *A. maculosus* was determined using only 5 specimens. The test lizard was placed in a beaker in an oven maintained at 45°C. After 15 minutes the temperature was raised at the rate of 1°C every 5 minutes. The average CTM for *A. maculosus*, derived from these five test animals, is 48.9°C. Two of these (one male, one female) recovered fully when the temperature was lowered after the test. The temperature from which there has been no recovery after cessation of muscular spasms has been recognised as the lethal temperature for this species.

The survival times at high temperatures have been regarded by some authors as more meaningful criteria and these have been determined for several Australian agamid lizards (Warburg 1965 a, b; Licht, Dawson & Shoemaker 1966; Bradshaw & Main 1968).

For *A. maculosus*, a survival time of 6.5 hours at 45°C was recorded, and over this period an 8% loss of body weight occured. Tests carried out at 42°C resulted in death between 22 and 25 hours following a loss of 6.8% of the body weight.

If death at this low level of body weight loss [cf. 34–48% loss at death for some iguanids (Hall 1922)] were due to desiccation only, it would indicate a rather low tolerance to desiccation for *A. maculosus* and its dependence on retreat to the humid region above the salt water-table of the lake. Further evidence of low desiccation tolerance has been observed in the vivarium where deaths occurred when the artificial "water-table" was not maintained and sub-surface humidity level dropped.

Evaporative water losses have been determined for a number of Australian lizards (Warburg 1965 a,b, 1966; Dawson *et al.* 1966; Bradshaw 1970). Attempts to measure evaporative water losses of *A. maculosus* were carried out using test animals either fresh from the field or which had been acclimated to a 24 hour cycle involving the attainment of temperatures in excess of their maximum voluntary activity temperature. Animals were tested between 1000 and 1500 hours, their most active part of the day.

The five animals tested varied from 8 g to 14.5 g in weight (mean 10.5 g). Although the measured EWL rate for *A. maculosus* varied, probably in relation to the degree of activity of the test animal, the average value was 1.10 mg/g/hr (0.8–1.5 mg/g/hr). Of this total EWL, pulmonary losses contributed 0.83 mg/g/hr (0.52–1.15) and 0.27 mg/g/hr (0.42–0.29) was due to cutaneous loss.

Bradshaw (1970) has found significantly lower cutaneous and pulmonary water loss in the desert-adapted *A. inermis* than in other species of *Amphibolurus* from more temperate habitats. His results suggest that the improved water economy of the desert-living species is due both to reduction in the metabolic rate and to alterations in the integument.

In Table 3 comparison is made between cutaneous and pulmonary water loss in *A. maculosus* and *A. inermis*.

The low proportion of total EWL attributable to cutaneous loss in the present figures

for *A. maculosus* suggests that the integument may be further modified against evaporative losses.

More detailed work is required to accurately define the critical ambient and body temperatures, and rates and sites of evaporative loss, in *A. maculosus*. However, available data do

TABLE 3

Rates of cutaneous and pulmonary water loss in A. maculosus *and* A. inermis

	A. maculosus	*A. inermis*
n	5	6
bodyweight	10.5g	24.1±0.97g
total EWL	1.10 mg/g/hr	1.05±0.0913 mg/g/hr
cutaneous	0.27 mg/g/hr	0.45±0.0931 mg/g/hr
pulmonary	0.83 mg/g/hr	0.57±0.0778 mg/g/hr
C/P	0.33	0.80

suggest that its temperature tolerance is among the highest known for Australian lizards, and that evaporative water losses are among the lowest recorded.

In its natural habitat, *A. maculosus*, like other heliothermic reptiles, uses a series of behavioural postures and movements to maintain body temperature within a preferred activity range. This activity range of temperature is higher in the field than the eccritic or preferred temperature selected by the lizards in a laboratory temperature gradient. However, except under some conditions imposed by the social hierarchy, the lizards can avoid intolerable heat levels by retreat to the damp sand of the burrow zone. Subservient males, kept away from the burrow zone by the dominant males, are forced to spend long hours on the salt surface with a consequent high level of body heat. Survival under these conditions must indicate the existence of physiological capacities to withstand high temperature and to restrict water loss. High body temperature is tolerated passively and water is conserved by lack of evaporative cooling mechanisms.

10. **Establishment and Defence of Territory by the Male.**

The early emergence, in late August, of dominant males of the previous season is usually preceded by these lizards positioning themselves just below the salt crust where they can more quickly respond to increasing temperatures. By mid-September the territories

established by these dominant males are under challenge by the younger males which have subsequently emerged. An old male challenged and displaced by a young male retreats underground for the remainder of the breeding season (September to late December). By mid-October the territorial situation has become fairly stable, and remains so throughout the breeding season.

Apart from the juveniles (snout-vent length <40 mm), three categories of male can be recognised in the dominance hierarchy.

(1) *Dominant:* lizards which exhibit display behaviour and fight and never retreat from another male. These lizards develop marked breeding coloration with bright orange-yellow ventro-lateral markings grading to brilliant reddish-orange ventrally with a pale patch mid-ventrally. The reddish-orange markings extend onto the base of the tail and under the thighs.

(2) *Sub-dominant:* lizards which exhibit display behaviour and which retreat instantly from a dominant male but will fight to a decision among themselves. Among these lizards a "peck order" is established despite their individual territories. These lizards also develop good breeding coloration.

(3) *Subservient males:* lizards which do not exhibit display behaviour, and which retreat from all other males or roll over into submissive posture on their backs if attacked. Only very faint yellow ventrolateral colours are developed by these lizards.

The territorial defence of the dominant males follows a classical pattern. Each territory is centred upon a look-out site, usually a small mound of salt 10–20 cm above the surrounding salt, or a piece of salt-encrusted driftwood embedded in the lake. The area of territories varies about an average of 15 m radius and is, in part, dependent on the virility of the controlling male. Orientation within their own territory and that adjacent to it is, at least partly, by sight and the boundary between the territory of two dominant males is known to those two males to an accuracy of a metre or so. The forcing of one male over the boundary immediately precipitates an approach and challenge from the adjacent male. This technique can be used to determine hierarchy patterns in the field in areas where territories of dominant males are adjacent. Male II will

flee if forced onto the territory of male I, but will fight (and win) against male I in his home territory.

The display behaviour of the dominant males involves a typical push-up movement in which the forelimbs are flexed and the whole of the forepart of the body moves. A short frog-like leap is followed by two quick push-ups. In challenging another male, the gular pouch is lowered and full threat display follows in which the body is raised high and compressed laterally so as to increase apparent size by enlarging the profile during a lateral confrontation (Fig. 12). This also displays fully the bright ventro-lateral markings. Usually the mouth is opened wide (Fig. 13). This display is usually adequate to deter intruders from entering the territory. When male to male fighting does occur an established pattern of events is observed. There is long-range recognition and challenge at distances of up to 14 m, then the commanding dominant closes the distance until a counter challenge is issued at a distance of about 3 m, after which the two males approach each other to a distance of about 0.5 m. There follows up to 10 minutes of bluff behaviour, side stepping, continual facing-up and counter-facing in an effort to get the tail into position to lash the opponent's head and forelimbs, and the head in a position where it is possible to bite the opponent's hind legs and back of the tail (Fig. 13). Head-on encounters also occur with the opponents' jaws becoming interlocked in tenacious biting.

In an eleven minute encounter, the longest observed, between males I and II in the hierarchy, three physical clashes occurred. The biting was directed at the hind limbs and each clash was over in an instant, the attacker being flung vertically by the momentum of the lunge and the evasive endeavour of the opponent.

There may be overlap in the territories established by the sub-dominant males. While the dominants remain "on guard" in their territory throughout most of the day, the sub-dominant males adjust their emergence times so that only one is active within the territory at one time.

Subservient males adjust their emergence times to periods when they are less likely to be pursued by the dominant males—in the heat of the day or late in the afternoon. Their level of tension in the presence of the dominant male is reflected in their respiration rate which may be as high as 120 breaths/minute as com-

pared with 35 breaths/minute for the dominant. They spend a very limited amount of time on the surface and then avoid recognition by flattening themselves, with head down, against the salt and remaining motionless for long periods. If challenged they immediately turn over onto their backs in submissive posture.

Once ground temperature exceeds the threshold the dominant males will emerge at about the same time ($\pm$10 minutes) each morning independent of light intensity or temperature. Heath (1962) records a similar temperature and light-independent emergence in *Phrynosoma*, suggesting the presence of endogenous circadian rhythm. During the breeding season this emergence time gets earlier by about 30 minutes each month. After the breeding season emergence becomes random and the dominant males generally spend more time underground. At this time there is an increase in activity of the subservient males which spend longer periods active on the surface of the lake. There is a lowering of tension between dominants and subservients (reflected in the fact that respiration rates are similar for both), and the subservients are less inclined to retreat underground or to remain "frozen" and thereby inconspicuous for long periods. Territoriality is not actively enforced after the end of December and, while the dominant male spends considerable periods underground, the subservient males embark on an active period of feeding which involves frequent excursions out over the lake in search of the ants which, at this time of year, constitute the main food item. In the absence of the dominants, the subservient males may establish territories between existing territorial areas.

The dominant males show a renewed burst of activity in early April, presumably feeding intensively before retiring underground. The dominant males and late developing females extend their activity period into May, whereas all others retire into torpor during about the third week of April.

The dominant males and the juveniles are the first to emerge and last to retire both daily and annually. Under vivarium conditions, with temperature maintained at 27°C for 12 months, the dominant males and juveniles remained active throughout the 12 months. The subservient and sub-dominant males and the females went into normal torpor despite the maintenance of temperature. These lizards emerged for 1–3 hours every 16–30 days. The

reason for these arousals from torpor is not known.

In the confined conditions of the vivarium, the dominance hierarchy of the "population" is established within about an hour. Hierarchical structure can be readily determined by observation of respiratory rates which range from 30 breaths/minute in the dominant male to 120 breaths/minute in the subservient males.

Carpenter *et al.* (1970) have described the display and aggression behaviour of three species of *Amphibolurus (A. barbatus, A. reticulatus inermis* and *A. muricatus)* and comment on the close similarity between the display patterns of these agamid lizards and the Iguanidae which have been more fully studied (Carpenter 1967). The display action patterns appear to be species-specific both in the Iguanidae and the Agamidae. The display patterns of *A. maculosus* have not been fully analysed but the same range of postural changes, involving head and forelimbs, described by Carpenter *et al.* (1970) have been observed. Brattstrom (1971) discusses the range of postures associated with social and thermoregulatory behaviour in *A. barbatus.*

11. Reproductive Behaviour

The adult females of *Amphibolurus maculosus* do not emerge until some weeks after the dominant males have established their territories. First to emerge at 21°–23°C in mid-September are the older females, followed, through to mid-October, by the younger females. The females establish burrows around the margin of the dominant male territories and do not, at this time, move far from the burrows. A small group of six to eight burrows, all within a metre or so of one another, usually indicates the presence of a female. At this time of year the burrows are frequently re-occupied and enlarged whereas later, in the hotter weather, a burrow is seldom used twice. During the first week or so after emergence the females are not ready for mating, and adopt two methods to repel the advances of a male. The first of these is circumduction. All females of reproductive size (>45 mm) circumduct with either forelimb in the presence of a male, and the rate of circumduction is accelerated if they are approached by the male or come into competition with the male for food (Fig. 14). Secondly, should circumduction fail as a deterrent, the female twists over on her back and lies immobile. Both these manoeuvres serve to distract the male by des-

troying the "female image" to which he has responded.

Most mating activity, and much of the territorial fighting, takes place at 34°–36°C, several degrees below the temperature (39°C) at which the body is maintained by thermoregulatory behaviour. Consequently during the mating season (October to December) greatest activity occurs between 0900 and 1100 hours. While feeding and territorial defence take place at 39°C, preoccupation with thermoregulation prevents sexual activity.

The male approach to the female usually begins with the male elevating his head to maximum height in order to confirm identification of sex. He then undertakes a series of energetic head-bobs, followed by one or two "frog-leaps" during his rapid approach to the female. A receptive female turns slowly from the oncoming male and waits to be overtaken. The male approaches the female directly from behind and with his jaws grasps her by a fold of skin just behind the occipital region. Using this nape grasp, the male rolls the female over on her side. With the tail of the male under the tail of the female, the cloacae lie close together and a hemipenis is inserted. The pair remain rolled on their sides for the duration of copulation (about 25 seconds) with the body of the female arched back with forelimbs clear of the ground (Fig. 15).

Following copulation, the female usually lies in a subservient position, with the head flat on the salt, for 15–20 seconds before moving. During this time the male "frog-leaps" away. Females undertake weak head-nodding during the breeding season, involving a simple dip and rise of the head. The exact purpose of this is unknown but, in view of the cryptic coloration, it may possibly serve to make known their presence to other lizards.

Following ovulation and fertilization, a number of changes occur in the appearance and behaviour of the females. In a fertilized female, ventro-lateral coloration changes from pearly-white to a bright orange-red, the edges of the lower jaw become orange, and there develop two orange patches between the forelimbs and two elongate orange patches along the flanks. Also circumduction ceases, and more efficient defensive behaviour is adopted. Upon the approach of a male, confrontation takes place with the female raising the head as high as possible and swivelling it around to prevent the male from getting over or past

her. If this fails, or if the male's approach is so rapid that this bluff is unlikely to succeed, the female rolls over onto her back, frequently well before the male makes physical contact with her (Fig. 16). Distracted by the changed image the male usually withdraws several feet, with some head-bobbing. After 15-20 seconds the female rights herself, inflates the gular pouch and stomach, and compresses the body to display the orange ventro-lateral surfaces and so present the largest possible profile to the male. The female then adopts a stiff-legged attitude which lifts the body clear of the substrate and with slow, deliberate steps advances straight towards the male. She usually passes close in front of him, often forcing him to withdraw a few steps or to transfer his body back on to the hind limbs, lifting the front part of the body to allow the female to pass close under his snout. After passing the male, the female continues to walk with the stiff-legged gait, stopping on each rise in the salt crust to look back at the male over her shoulder. When about 6 m away, her pace quickens and finally she relaxes and runs at high speed over the salt to disappear behind a fold of the salt crust.

In contrast to their timidity early in the season, females, once fertilized, become quite aggressive and will attack a male should he compete for food at close quarters. While carrying developing eggs the female emerges at the same time as the dominant males and spends maximum possible time in basking postures. Perhaps the orange ventro-lateral coloration of the female at this time increases heat absorption from the substrate. Ventral colour change in the gravid female has been reported in the American lizard *Crotaphytus collaris* by Fitch (1956) and in *Callisaurus, Cophosaurus* and *Holbrookia* by Clarke (1965).

Eggs are laid 20-25 days after fertilization. The female digs a distinctive burrow for egg-laying. Normally these lizards merely nose their way under the salt crust and "swim" at a shallow angle through the fine, dry drift sand, down to the damp consolidated substratum. The egg-laying female carefully selects a site, usually along the shore-line, of consolidated sand damp right to the surface. This egg-laying burrow is steeply angled (about 45°), extending down 21-25 cm, with a distinct chamber at the bottom in which the eggs are deposited. Young females lay only 2 eggs while older females produce 3 or 4. After deposition of

the eggs the entrance to the burrow is filled in again. Observations, both in the field and in the laboratory, suggest that each female digs and fills several egg-laying burrows before she finally deposits the eggs. Whether abandonment of these early burrows is due to disturbance or whether there is careful selection of some particular set of conditions, is not known. The salt content of the shore-line sand is 4-5% and this, apparently, does not impede development of the eggs. Attempts to hatch eggs under laboratory conditions indicate that maintenance of fairly high humidity during egg development is important. Females frequently emerge from egg-laying in poor condition and highly desiccated (Fig. 17). The ventro-lateral colouring fades from orange to yellow to white after deposition of the eggs.

Hatching occurs after about 70 days and the hatchlings (SV length 25-30 mm) first appear in January and continue to emerge until April.

12. Sex Recognition

In most animals showing marked sexual dichromatism it is the male which is more brightly coloured or strongly marked. On this basis it was accepted, in early stages of this study, that large specimens of *Amphibolurus maculosus* with bright yellow-orange-red ventro-lateral surfaces were male and that this brilliant colouring was a key factor in the signal pattern of male to male sex recognition in territorial behaviour. The sex of tagged lizards was recorded on this basis of presence or absence of ventrolateral coloration.

Recapture of marked specimens revealed two stages of development at which colour changes confused this simple interpretation. Firstly, there is the change from pseudo-female to male colour and behaviour at the time the male reaches the size of an adult female. In some cases, specimens showing weak male coloration were observed to show the usual female responses of circumduction and tonic immobility. On dissection, lizards of this group (all within 43-58 mm SV length), proved to be male. Recapture records revealed that, up to 58 mm SV length, the first-year males of *A. maculosus* show the yellowish ventro-lateral markings typical of the female after egg-laying. Lizards of this size (up to adult female size) and coloration are repeatedly identified as female by the dominant males and are driven out to the margins of the colony by the repeated unwanted advances of the males. This

suggests a possible dispersal mechanism within the population.

Secondly, some lizards which had been initially recorded as female, on subsequent recapture showed brilliant ventro-lateral coloring. Allied with change of colour, there was a change in behaviour with these lizards now counter-challenging an approaching male. This change from nearly-white female to brilliant orange pseudo-male coloration and the change in defensive behaviour and aggression following ovulation and fertilization have been described previously.

While sexual dichromatism exists, observations suggest that coloration has little if anything to do with sex recognition in *A. maculosus*. The female undergoes considerable change in intensity of coloration from complete lack of ventro-lateral coloration through pale yellow to brilliant orange after mating, but is pursued by the dominant males at all stages in the development of this colour pattern.

A first-year male, on the other hand, may show typical male colouring, with prominent rusty spots on the shoulders and weak gular pouch stripe and yet be repeatedly mistaken for a female. Thus, first-year males, whether they have developed male coloration or not, are recognised as female within the first-year female size range of 46–58 mm.

In an effort to determine the role played by colour in sex recognition, and to determine what colour pattern might act as an innate releasing mechanism in territorial display, dominant males in the vivarium were presented with a range of coloured models, simulating male coloration. None of these elicited any response other than an investigatory lick.

The above observations suggest size to be the basic factor involved in sex recognition and suggest that size judgement is particularly good.

In relation to elevation (most look-out sites in the habitat of the lizards are no more than 20 cm above the lake surface), *A. maculosus* shows remarkably acute vision. Observations of territorial challenges in the field have indicated that these lizards have perception of movement and recognition of posturing at distances of 50 metres.

Both laboratory and field observations indicate that there is some individual recognition between members of the line hierarchy established in the vivarium and between males of adjoining territories in the field population.

TABLE 4

Relationship of size to age in Amphibolurus maculosus

	Mean SV length of *A. maculosus* (mm)	
	Female	Male
1st year	48	54
2nd year	59	64
3rd year	61	67
4th year	62	70

This significance of size and accuracy of size perception would also be a a key factor in the effectiveness of the bluff behaviour. Unless the lizards had such an appreciation of size and its significance, the act of increasing the area to view by enlarging the lateral profile would not be effective as a bluff deterrent.

13. Growth Rate and Reproductive Cycle

Over the period of study, 376 body measurements (SV length and tail length) were recorded for marked and unmarked specimens.

Based on field recapture of marked specimens and vivarium specimens for which age histories were known, mean SV lengths of *Amphibolurus maculosus* in relation to age are shown in Table 4. The figures represent the mean maximum measurement recorded at the end of the active season for each year. Mean SV length of hatchlings is 30 mm. It seems likely that *A. maculosus* dies at the end of the third breeding season, at 3–3½ years. No older specimens have been recovered among the marked population at Lake Eyre.

When adult males emerge at the beginning of the season in September, the testes are fully expanded (9 x 5 mm). Smear tests show active spermatogenesis from September through to mid-December and active sperm have been found in the vas deferens in October, November and December. In late December there is a rapid contraction in size of the testes to 6 x 3 mm. No active sperm have been found in testes or epididymes from January to April. This decline in male fertility coincides with the onset of the period of reduced activity in the males. Between late December and early March the older males spend only short periods on the lake surface and longer periods underground. At this time, young males move back into the territorial area, subservient males emerge for longer periods and they and the females, exhausted after egg-laying, embark on long hours of feeding. There is little territorial defence, the dominant males only weakly

TABLE 5
Summary of reproductive cycles in Amphibolurus maculosus

	Dominant Male	First yr. male	First yr. female (A)	First yr female (B)	Adult Female
January	Inactive	Active feeding	Hatching	Ovulation	Active feeding.
February	Inactive				
March	Active feeding	Hatching		Egg laying	
April	Active feeding Testes and fat bodies expand			Hatching	
May					
June	Hibernation				
July		Hibernation	Hibernation	Hibernation	Hibernation
August	First emergence				
September	Establishment of territory. Spermatogenesis				
October	Spermatogenesis Mating with adult females	Identified as female. Retreats to edge of territorial area			Ovulation Mating Colour change to pseudo-male
November	Spermatogenesis Mating with adult females		Ovulation		
December	Spermatogenesis Mating with 1st year females. Contraction of testes	Returns to territorial area	Mating Egg-laying	Mating	Egg-laying

defending (with a slight lowering of the gular pouch) a small area immediately around their burrow site.

The older males show a more active feeding period through mid-March and April. During this time the testes, together with abdominal fat bodies, expand rapidly prior to the onset of hibernation.

Information from recapture of tagged specimens, as well as laboratory observations, indicates that among the first-year females of the population there is a bimodal pattern of ovulation.

Females hatched during January-February ovulate in November-December. A second series of females, hatching late in April, ovulate in February. Both these groups of females show maturity (as evidenced by ovulation) at 10 months. Of these 10 months, at least 4 winter months (May, June, July and August) are spent in torpor. In the earlier part of the active breeding period (October to December) the dominant males mate with the adult females. Towards the end of the breeding period the 1st-year females, down to 46 mm SV lengths, are successfully mated by the dominant males.

Sperm retention in the female is indicated by the decline of male fertility in December and the fact that ovulation in the late-hatched females, which had been mated in December, does not ocur until February. In March these females lay eggs which hatch in April.

The males hatched in January and February are sub-adult (with female coloration and behaviour) in November-December. Table 5 summarises male and female reproductive cycles of *A. maculosus*.

CAPTIONS TO FIGURES 4-17

Fig.   4. *Amphibolurus maculosus*, showing detail of the head with deeply sunken eye, visor-like eyelid, and absence of visible tympanic membrane.

Fig.   5. Margin of Lake Eyre, looking north towards Prescott Point at the tip of Sulphur Peninsula. Instruments recording continuous air and sub-surface temperatures are set up in the burrow zone area. The beach is backed by low white sand dunes and to the left the thin distorted crust of the burrow zone merges into the thicker, smoother salt crust of the "wet" salt zone.

Fig.   6. View back along the causeway towards Prescott Point (October, 1966). Quadrats were set up along this causeway and movements of tagged lizards were recorded in the area over several years.

Fig.   7. Buckled surface of salt crust on Lake Eyre. View towards Prescott Point.

Fig.   8. Nests of the ant, *Melophorus* sp., are regularly spaced through the "wet" salt zone. The above-surface mounds of these nests are visible here as dark spots (from their shadows) in contrast to the white salt surface.

Fig.   9. *A. maculosus* male against the disturbed base of *Melophorus* nest-mound. These mounds are used for basking and shelter and as vantage points by the lizards.

Fig. 10. *A maculosus*, overheated by pursuit, showing panting reaction typical at raised body temperatures. Note deep "lens-hood" protection for the eyes.

Fig. 11. Salt clods on digits of a forelimb.

Fig. 12. Dominant male in full threat display. Body raised and laterally compressed, gular pouch and stomach inflated.

Fig. 13. Dominant males fighting. Specimen in background shows compressed and raised body, gular pouch lowered, and mouth open for biting. The tails are brought into play to whiplash the head and forelimbs of the opponent. (Dark areas at base of tail are identification marks.)

Fig. 14. Circumduction by *A. maculosus* female.

Fig. 15. *A maculosus* in copulation. The male biting and holding the female by skin fold behind the head.

Fig. 16. *A maculosus* female (left) showing post-fertilization colour development on lower jaw (the under abdomen is also bright orange) and the typical defensive position relative to the male on the right.

Fig. 17. Female, after egg-laying, showing lateral skin flaps under conditions of starvation and dehydration.
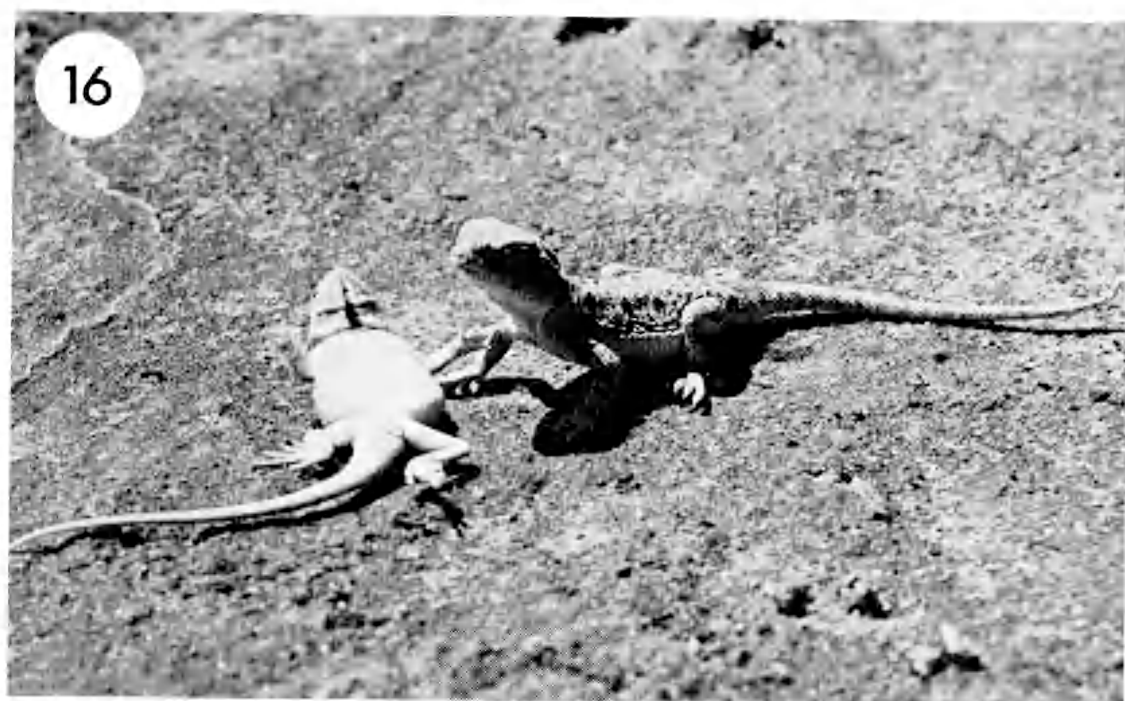
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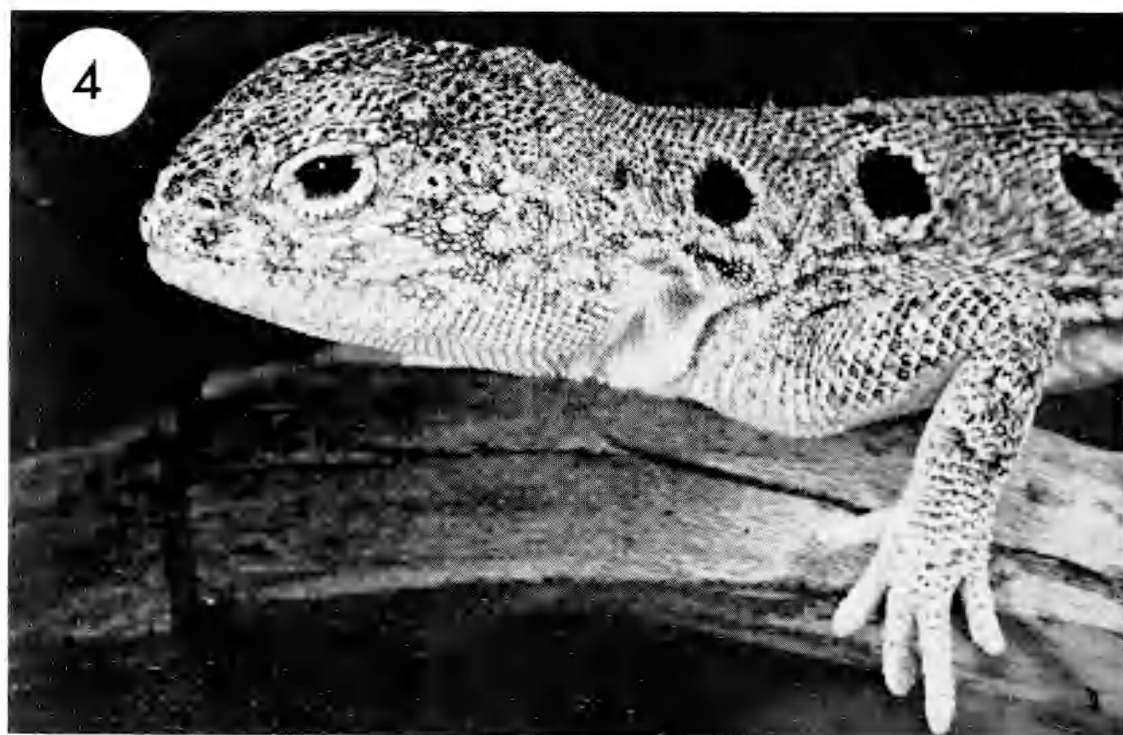
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